Pollination does not affect floral nectar production, and is required for fruit-set by a hummingbird-visited Andean plant species

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ABSTRACT

Copious red nectar is produced in the flowers of *Jaltomata calliantha* (Solanaceae), a rare, herbaceous perennial native to Andean Peru. In greenhouses we determined that although self-compatible, flowers are not autogamous: pollination by an external vector is required for fruits to be set. Nectar is produced in all flowers, up to 94 µl per flower per day, first as nearly clear liquid, and then turning bright orange to red. Total nectar production over the life of a flower (with daily removal) ranged from 20–133 µl. Hand-pollination does not affect the rate or total volume of nectar produced. Published on-line www.phytologia.org *Phytologia 98(4): 313-317 (Oct 6, 2016)*. ISSN 030319430.

KEY WORDS: floral corona, fruit-set, *Jaltomata calliantha*, nectar volume, pollination, red nectar, self-compatible

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The genus *Jaltomata* (Solanaceae) includes 70 species distributed from Arizona, USA, through Central America and Andean South America (Mione et al., 2015a, 2015b, 2016). The focus of this study was on *J. calliantha* S. Leiva & Mione, a wild, herbaceous perennial restricted to only two known locations in Peru. Flowers of *J. calliantha* are visited by hummingbirds in the more northern of the two populations (Department La Libertad). Only fruits were present (no flowers) when this species was collected in Department Ancash, and thus the floral visitors of this population are unknown. Given that colored nectar is correlated with vertebrate pollinators, mainly birds (Hansen et al., 2007), and that the flowers of the two populations are indistinguishable, it is likely that both populations are pollinated by hummingbirds. Flowers are solitary, and pistillate for about a day before the anthers dehisce. The corolla is green and 3–4 cm across. The floral corona (Figure 1A, left arrow) creates nectar troughs between the stamens. Floral nectar is amber in color when the flowers open (Figure 1A), but darkens with age becoming conspicuously orange to blood-red (Figure 1B), apparently serving as an attractant and reward to pollinators.

Animal pollinators are a requirement for sexual reproduction by 60–90% of plant species (Kremen et al., 2007). If pollinators are lost (regionally extirpated or extinct) due to habitat loss or climate change, how will biotically pollinated species fare? With this question in mind, we explored the question of whether pollination is required for fruits to be set by this Andean species, or if flowers automatically self-pollinate (autogamy) and set fruit in the absence of an external pollen vector. Given that nectar production is energetically expensive (Pyke, 1991), we also offered the hypothesis that a physiological mechanism might have evolved to decrease or cease nectar production following pollination.
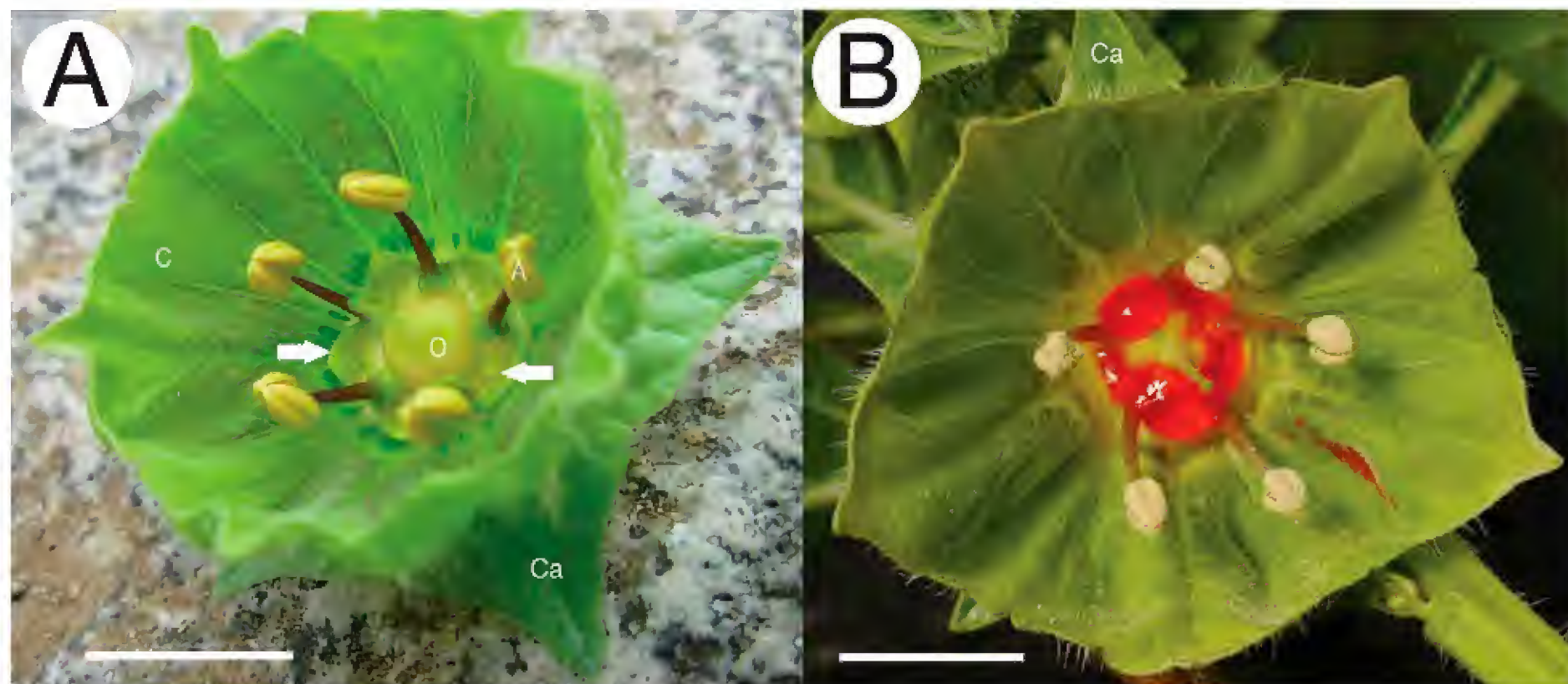
Figure 1. *Jaltomata calliantha.* **A**—Pistillate-phase flower: left arrow - corona, right arrow - the first nectar produced is amber in color, Ca - calyx, C - corolla, A - anther, O - ovary. Bar length = 1 cm, *Mione et al. 758*, photographed by T. M. in Peru. **B**—Hermaphroditic-phase flower: Ca - calyx, nectar is bright red at center of flower. Bar length = 1 cm. *Mione et al. 855/856*, photographed by T. M. at Central Connecticut State University.

MATERIALS AND METHODS

Seeds were collected in the wild in Peru, from 1379 to 2100 m elevation in Department Ancash (*Mione et al. 855 & 856,* CCSU) and treated with gibberellic acid (300 ppm) for 20 hours to induce germination. Plants were grown in greenhouses at Central Connecticut State University. Prior to anthesis pairs of flower buds from the same plant were tagged on the same day, 21 pairs divided nearly equally among five plants. The first day that the flowers opened, while still in their pistillate phase, one randomly chosen flower of each pair was hand-pollinated and the other flower remained unpollinated (the control). Given that anthers of a given flower have not yet dehisced during this pistillate phase, pollen for hand-pollinations was taken from other hermaphroditic-phase flowers on the same plant (i.e., geitonogamous pollination). Nectar was extracted and measured with volumetric microcapillary tubes from all flowers at nearly the same time each day, until flowers ceased producing nectar. This procedure continued until the corolla senesced, which was usually after five days. Flowers were revisited after three weeks to assay for fruit-set, but one branch had broken, reducing the number of flower pairs to 20.

RESULTS AND DISCUSSION

Ninety percent (18/20) of the flowers that were manually self-pollinated set fruit (Figure 2) containing the usual number of full-sized seeds, but none of the unpollinated (control) flowers set fruit. Obviously, the null hypothesis of equal fruit-set from pollinated vs. unpollinated flowers was rejected (Wilcoxon matched-pairs signed rank test, two-tailed, $P < 0.0001$). These tests demonstrate self-compatibility given that the source of pollen was always the same plant. Hand-pollinated flowers received pollen prior to anther dehiscence, and thus this fruit-set certifies stigma receptivity during day one (prior to anther dehiscence). Consequently, we refer to the phase prior to anther dehiscence as the pistillate phase. We refer to the following phase as the hermaphroditic phase because the stigma is also receptive after anthers dehisce (Mione, unpubl. data).
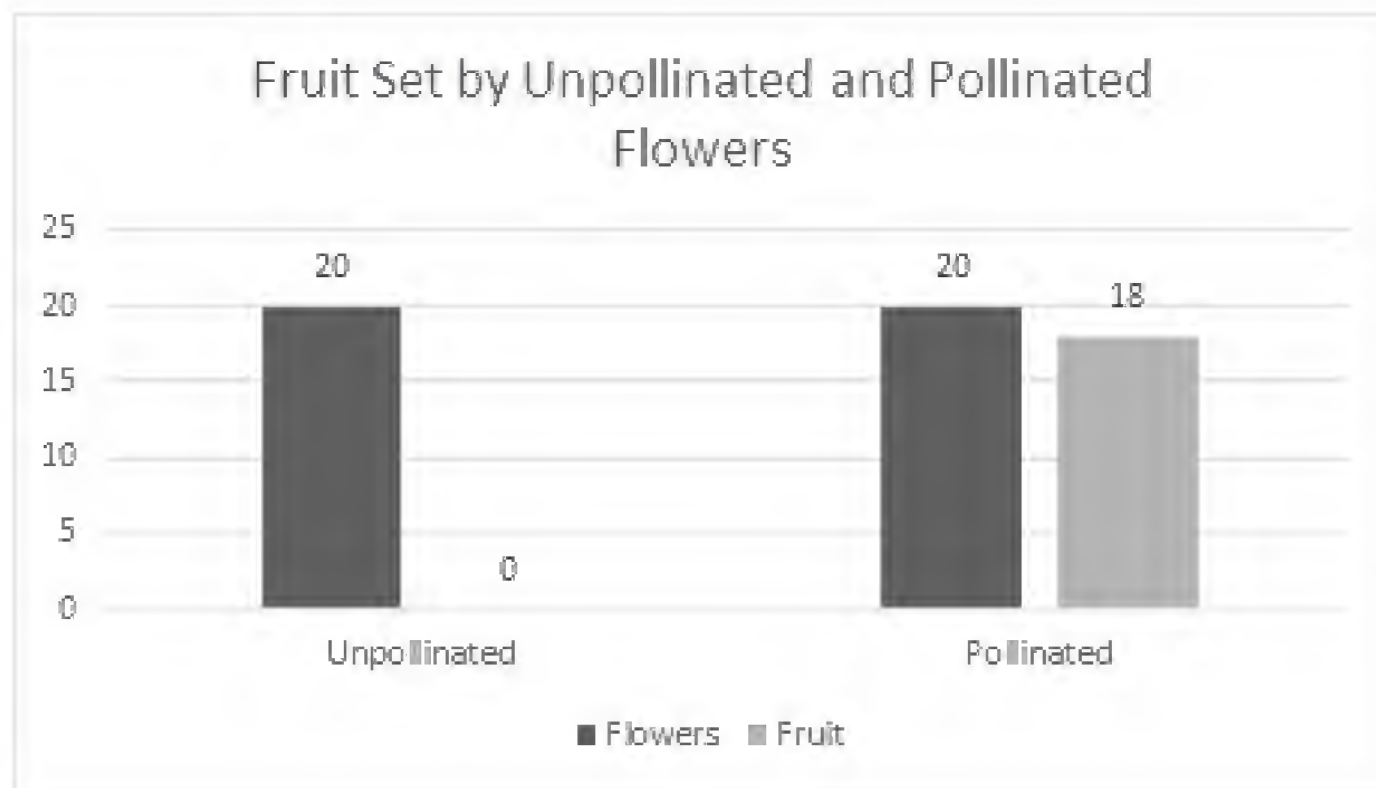
Figure 2. Fruit set by unpollinated (control) versus hand-pollinated flowers.

Considering both 21 pollinated and 21 unpollinated flowers, daily nectar production ranged from 0–94 μl. The average total nectar volume (over the life of the flower, with daily removal) was 52 μl, ranging from 20–133 μl (Figure 3). Variation in nectar production among flowers of the same plant is expected (Pleasants and Chaplin, 1983). The nectar volumes we measured suggest that *Jaltomata calliantha* provides a considerable supply of water and calories to floral visitors, and are similar to those measured for other hummingbird-pollinated flowers (Stiles and Freeman, 1993; Fonseca et al., 2015). Hummingbirds have been observed visiting the flowers and feeding on the floral nectar of *J. calliantha* in Peru (Mione & Leiva González, field observation).
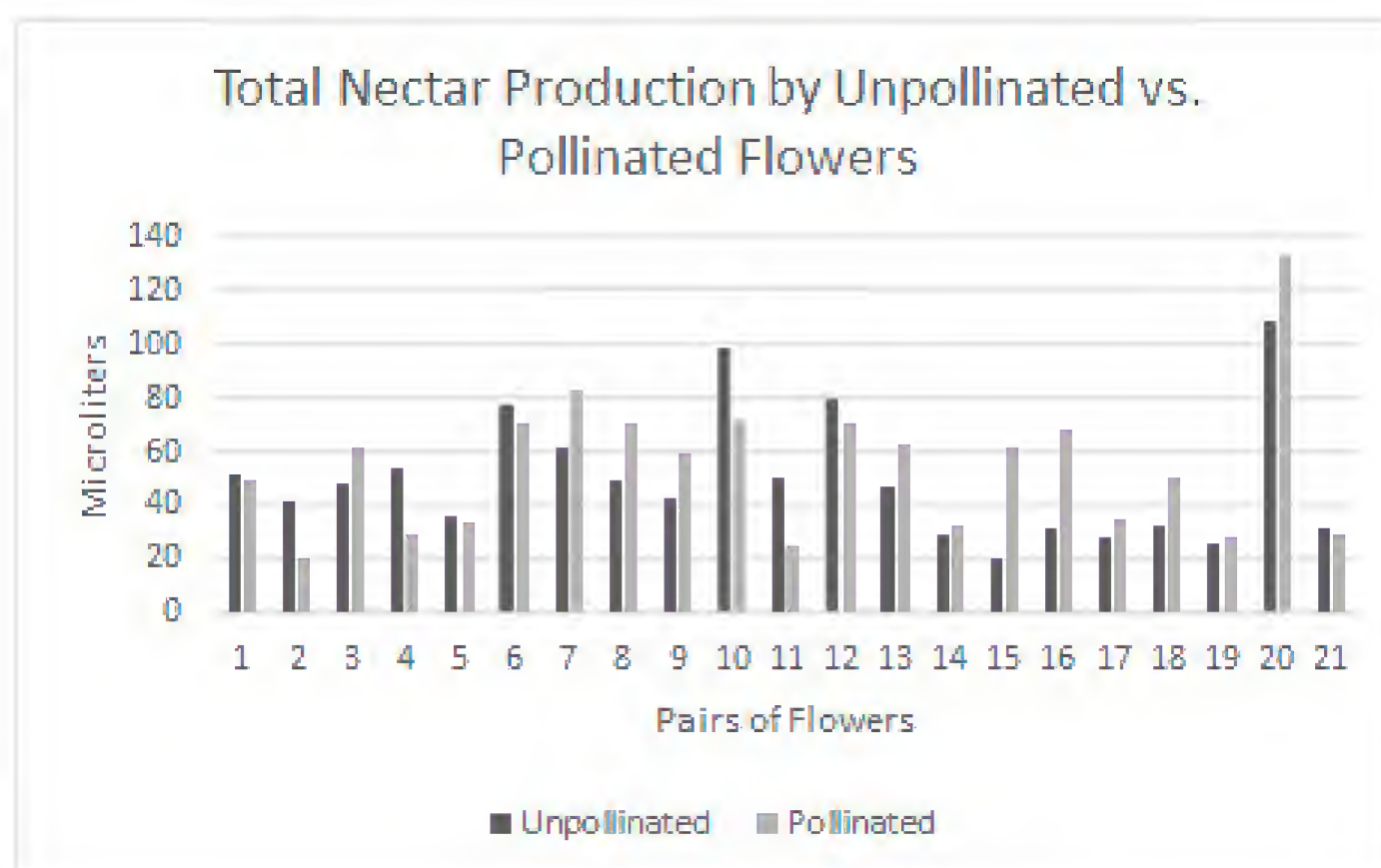

Figure 3. Total nectar production in unpollinated (control) versus hand-pollinated flowers.

Pollination has no effect on nectar production. Nectar volume in pollinated vs. unpollinated flowers is not significantly different (each pair of observations was on the same plant, with one flower pollinated and the other untreated, paired two-tailed T-test, P=0.2744, df = 20). However, during our study water was never limiting, and results may be different in the field where resources are likely scarce

at times. Aizen and Basilio (1998), studying a bumblebee-pollinated Andean, perennial herb (*Alstroemeria aurea*), and Delph and Lively (1989) studying a bird-pollinated tree (*Fuchsia excorticata*) of New Zealand, both found that hand-pollination had no effect on nectar production. In contrast, Stpiczyńska (2003) found that pollination actually increased nectar production in an orchid species.

As noted above, while 90 % of hand-pollinated flowers produced fruit, none of the 20 unpollinated flowers set fruit. Some 180,000 flowering plant species completely rely on biotic pollinators for their survival (Bodbyl Roels and Kelly, 2011). This rare plant may be vulnerable to extinction if it loses its pollinator or pollinators to habitat loss or to global warming (Buermann et al., 2011). At least 1,000 of the nearly 200,000 angiosperms that rely on biotic pollinators are used for agriculture (Bodbyl Roels and Kelly, 2011); thus, like the *Jaltomata* we studied, understanding the biology of pollination and protecting both the plants and their pollinators is not only important, but, for our crops, critical.

CONCLUSIONS

Jaltomata calliantha produces copious bright-red floral nectar (Figure 1B) that may serve as both an attractant and a reward to the hummingbirds that visit its flowers in the Andes. Continuous nectar production likely results in multiple hummingbird visits enhancing both female and male reproductive success (Fenster et al., 2006). Although self-compatible, flowers are not autogamous: pollination by an external vector is required for fruits to be set. In greenhouses hand-pollination does not affect nectar volume.

ACKNOWLEDGMENTS

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